

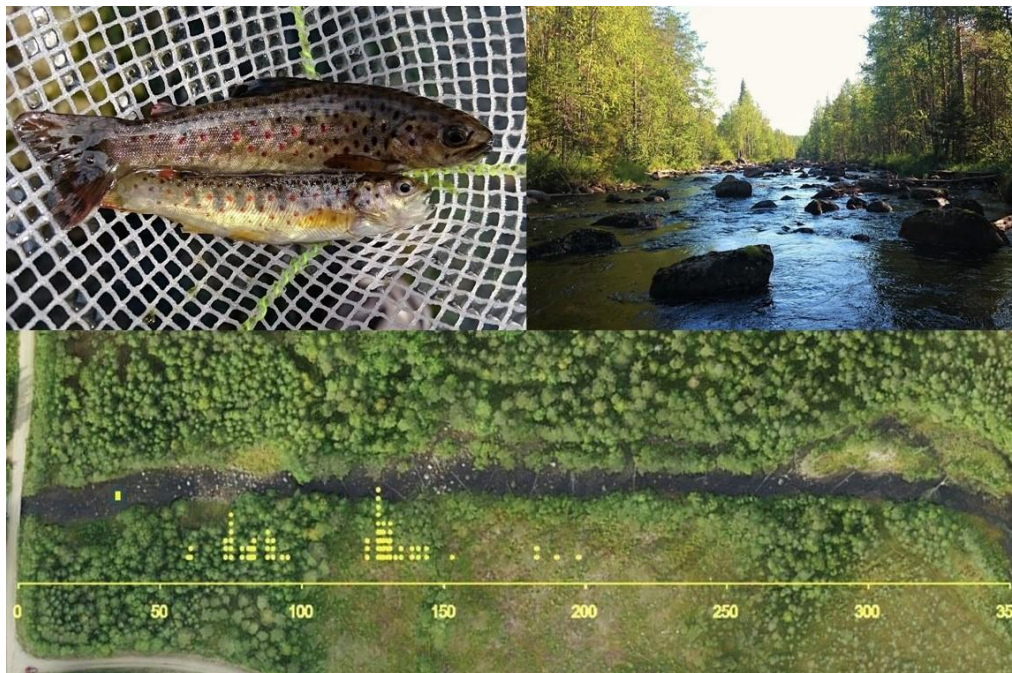
Dispersal of young-of-the-year brown trout (*Salmo trutta* L.) from spawning beds

- Effects of parental contribution, body length and habitat

Spridningsmönster hos årsyngel av öring (*Salmo trutta* L.) från lekbottnar

- Effekter av föräldrapar, kroppslängd och habitat

Susanna Andersson



Examensarbete i ämnet biologi

Department of Wildlife, Fish, and Environmental studies

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Susanna Andersson

Supervisor: Daniel Palm, Dept. of Wildlife, Fish, and Environmental Studies

Assistant supervisor: Gustav Hellström, Dept. Of Ecology and Environmental Sciences

Examiner: Eva Brännäs, Dept. of Wildlife, Fish, and Environmental Studies

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Sveriges lantbruksuniversitet
Swedish University of Agricultural Sciences

Faculty of Forest Science
Department of Wildlife, Fish, and Environmental Studies

Abstract

Stocking of brown trout eggs *Salmo trutta* L. and construction of spawning beds are common measures in habitat restored streams. However, knowledge about how young-of-the-year (YOY) trout disperse from stocking points and spawning beds, and how it relates to biotic and abiotic factors, are sparse. This study was conducted to explore dispersal differences among families, if dispersal is restricted to a limited area, if habitat characteristics have an impact on the dispersal, and if trout managers have to take YOY trout dispersal into account for successful restoration. Dispersal of YOY trout was investigated at the end of the first growing season in a stream in northern Sweden where the former trout population had been depleted. Trout eggs from eight families were stocked in three stocking points in March 2015. In August and September 2015 the trout were located by the means of electrofishing. Body length was measured and tissue samples were collected from the anal-fin. A DNA analysis using Single Nucleotide Polymorphism (SNP) markers was conducted to confirm origin of the individuals. More individuals were dispersed downstream than upstream and the majority of the individuals stayed within a distance of 200 m from the stocking point. Body length and dispersal direction did not have any effect on the distance dispersed. Only one of the families showed a different dispersal pattern than the others, individuals did not stay in the direct vicinity of the stocking point and were aggregated further downstream than other families. Habitat characteristics were found to have an impact on the number of trout located at specific stream sections and on the dispersal distance. These findings can make restoration projects more successful as they facilitate trout managers to find strategic egg stocking points.

Sammanfattning

Vid habitatrestaurering av vattendrag är återskapande av lekbottnar och utsättning av öringsrom *Salmo trutta* L. vanliga åtgärder. Dock är kunskapen om hur årsöringar sprider sig från lekbottnar och utsättningspunkter, och hur det kan relateras till biotiska och abiotiska faktorer, begränsad. Denna studie har utförts för att undersöka spridningsskillnader mellan familjer av öring, om spridning är begränsad till ett specifikt område, om habitat har en påverkan på spridning och om hänsyn bör tas till årsöringars spridningsmönster i restaureringsprojekt. Årsöringarnas spridning undersöktes i slutet av första tillväxtsången i ett vattendrag i norra Sverige som inte hade någon befintlig öringpopulation. I mars 2015 sattes rom från åtta familjer ut i tre olika utsättningspunkter. Under elfisken i augusti och september 2015 mättes öringarnas kroppslängd och vävnadsprover togs från analfenan. En DNA analys utfördes med hjälp av Single Nucleotide Polymorphism(SNP)- markörer för att fastställa vilka familjer individerna tillhörde. Fler individer spred sig nedströms än uppströms. Majoriteten av alla individer spred sig inte längre än 200 m från utsättningspunkten. Kroppslängd och spridningsriktning visade sig inte ha någon effekt på spridningsavståndet. En av familjerna uppvisade ett avvikande spridningsmönster i jämförelse med de andra familjerna, individerna stannade inte i utsättningspunktens direkta närhet och de var aggregerade längre nedströms än de andra familjerna. De undersökta habitatvariablerna visade sig ha en påverkan på antalet öringar i habitatet och spridningsavståndet. Resultatet av denna studie kan underlätta vid restaureringsarbeten genom att fungera som underlag för lämplig placering av romutsättningspunkter.

Introduction

Dispersal of YOY trout (*Salmo trutta* L.)

In general, knowledge about salmonid biology is comprehensive, both regarding adult and juvenile life stages. This is promising as it aids future management of the populations. However, when it comes to the specific life-stage from swim-up and the following three months when fry disperse, knowledge is still inadequate in some salmonid species.

Dispersal patterns of young salmonids from the redd or stocking point have been related to several factors e.g. water velocity, velocity changes, and fry size. When young salmonids leave the gravel they have not yet possessed full swimming capacities (Elliott, 1987, Beall et al., 1994). This makes trout fry sensitive to velocity changes and they can easily be swept away in a downstream direction (Ottaway and Clarke, 1981, Elliott, 1987, Daufresne et al., 2005). Studies have found that downstream dispersal had a positive relationship with velocity (e.g. Ottaway and Forrest, 1983, Crisp and Hurley, 1991, Saltveit et al., 1995). Downstream dispersal has also been found to have a negative relationship with the size of the fry. This was found in a study by Heggenes and Traaen (1988) on four salmonid species in experimental channels. Also, in another study by Héland (1980) fry that had dispersed downstream were smaller than those that had stayed close to the redd. However, no significant difference in size between upstream and downstream migrants was found in a study of Atlantic salmon *Salmo salar* L (García de Leaniz et al., 2000). Intense competition for food and space after emergence can lead to downstream drift of fry. Several studies show that the main part of salmonid fry disperse downstream and only a fraction disperse upstream (e.g. Beall et al., 1994, García de Leaniz et al., 2000).

Webb et al. (2001) has studied Atlantic salmon fry around 17 weeks after hatching and found that the largest distance travelled was 90 m upstream and 940 m downstream from the stocking point. Most fry had dispersed downstream within the distance of 380 m from the redd. Webb et al. (2001) also found a difference in dispersal pattern between families of Atlantic salmon.

Only a few studies, e.g. Thorpe (1974) and Elliott (1987), have focused on how young-of-the-year (YOY) brown trout disperse from spawning beds. Thus, knowledge about distance dispersed by young brown trout still remains lacking (Saltveit et al., 1995). Also, no studies have investigated if the dispersal patterns of brown trout differ in different habitats or between families.

Restoration of streams used as floatways

Several Swedish streams were adjusted during the 19th and the first half of the 20th century to facilitate the transport of timber (Bernes, 2011). They were used as floatways for timber and to ease the timber transport they were systematically channelized and straightened (Näslund, 2000). Boulders were removed, side channels were closed and dams were built (Näslund, 2000, Törnlund and Östlund, 2002, Bernes, 2011). The extensive alteration of the streams has had a negative impact on the whole ecosystem and especially on stream dwelling organisms (Näslund, 2000, Bernes, 2011). Since the 1980s' extensive work to restore these streams has taken place. Measures, such as, replacement of boulders, re-opening of side-channels, replacement of large woody debris (LWD) and construction of spawning beds are carried out to recreate habitats for organisms such as the brown trout (Nilsson, 2006). To further improve the chances of the brown trout populations to

recolonize these streams, fry and eggs are stocked in restored streams (Barlaup and Moen, 2001, Luhta et al., 2012, Syrjänen et al., 2015).

The ability of the fry to disperse is generally not considered during stocking or during the creation of new artificial spawning beds in restoration projects. This potentially causes very high competition among fry in some habitats while some habitats remain unused. To make the restoration projects more cost-effective the spawning beds should be allocated with consideration to the dispersal ability of the fry.

Aim

This study aim to compare the dispersal distances after the first growth season between three different stocking points and between eight different families of brown trout. Dispersal distances will then be related to YOY body length and mesoscale habitat characteristics. The aim is also to discuss these findings in relation to how spawning beds are allocated in restoration projects.

The following four questions will be addressed:

- Do YOY trout disperse differently between families?
- Is YOY trout dispersal restricted to a limited area?
- Does mesoscale flow and habitat characteristics influence YOY trout dispersal?
- Do trout managers need to consider YOY trout dispersal patterns for successful restoration?

Materials and Method

Study site

The study was conducted in the stream Falåströmsbäcken (64°50'47.5"N 18°34'52.9"E) which is a third order stream in the catchment of Ume river and Vindel river (Fig. 1). Falåströmsbäcken is an about 2 km long tributary to Vindel river that runs from Lake Österavan to Lake Ruskträskkalven. The study site reaches from the outlet of Österavan and 1 540 m downstream (Fig. 2).

The stream was used as a log float way until the mid-20th century. To simplify log transporting, the stream was channelized and large boulders were removed. A splash dam was also constructed at the outlet of Lake Österavan. This caused a reduction in the suitability of the stream as a spawning and nursery habitat for salmonids. Potentially, this also caused the extinction of brown trout in the stream. Restoration of the stream took place in 2004 when the dam was removed. In 2010 boulders and LWD were reintegrated, side channels were re-opened, and spawning beds were recreated.

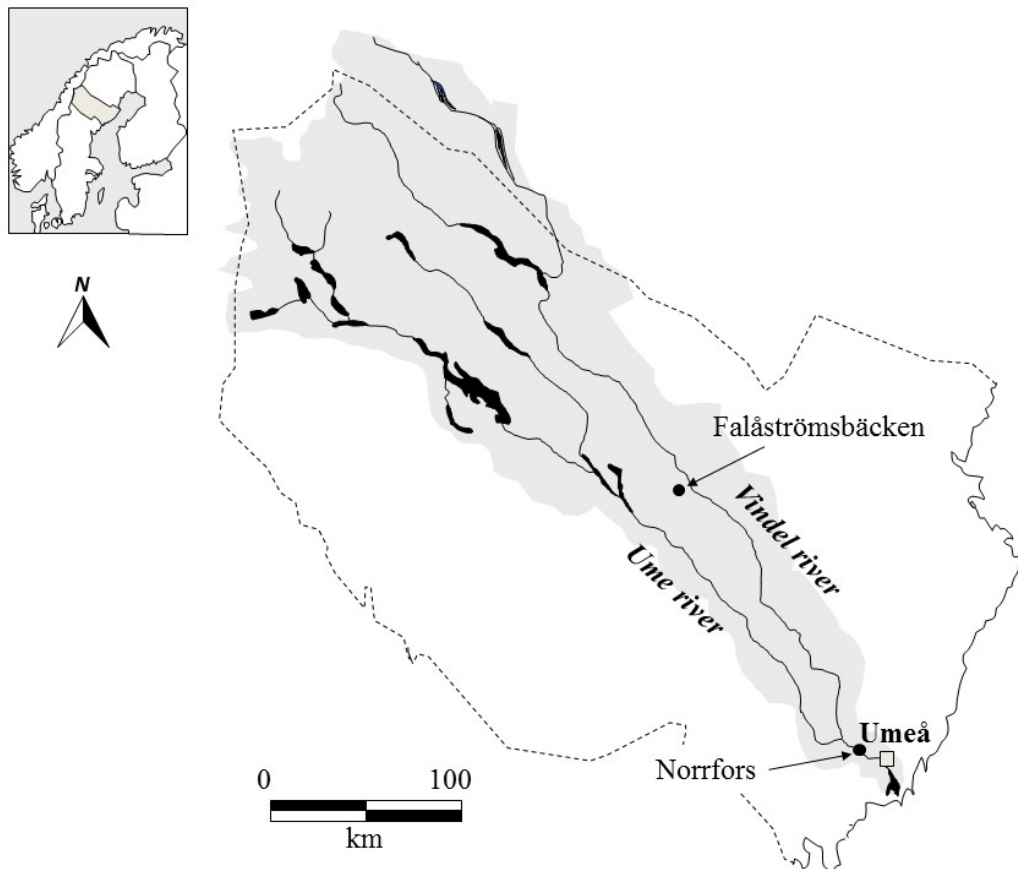


Figure 1. Map showing the location of Falåströmsbäcken and Norrfors fish ladder in Ume river and Vindel river catchment in northern Sweden.

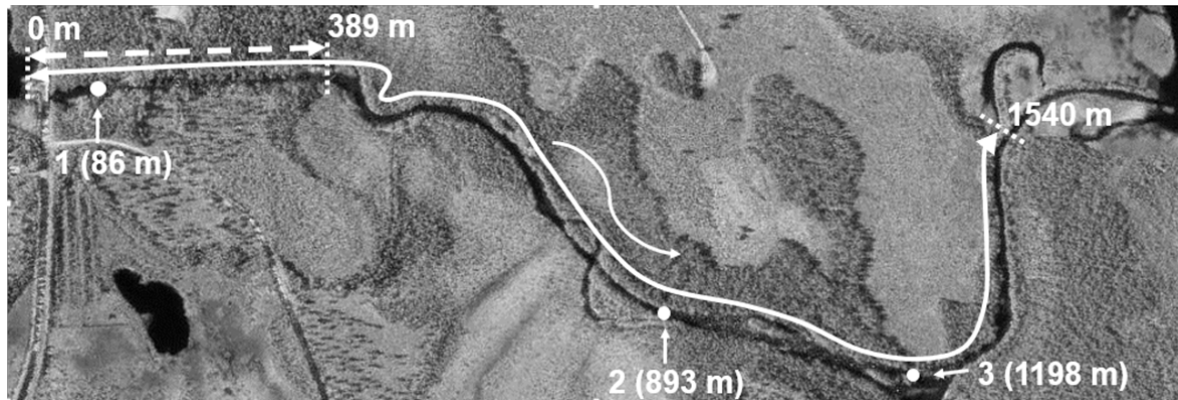


Figure 2. Aerial photo of Falåströmsbäcken. Numbers and dots indicate the location of the three stocking points and their distance (m) from Lake Österavan. The solid white line indicates the electrofished distance in August and the broken white line represents the electrofished distance in September. Lake Österavan can be seen on the left and Lake Ruskträskkalven on the right. The small, curvy arrow indicates direction of stream flow.

Before the experimental introduction of brown trout, bullhead *Cottus gobio* L. was the predominant species in the stream. However, low numbers of perch *Perca fluviatilis* L., burbot *Lota lota* L., pike *Esox Lucius* L., common roach *Rutilus rutilus* L. and brook lamprey *Lampetra planeri* Bloch. were also present. The brown trout spawning phase in streams in vicinity of Falåströmsbäcken occur in September and October (Svensson, 2012).

The average mid-channel depth was 0.5 m, average channel width was 11.9 m (SvensktElfiskeRegiSter (SERS), 2015) and discharge ranged between 0.6 to 3.3 m³ s⁻¹ in 2015 (SMHI, 2016). The water velocity is variable along the stream with both pools and riffles being present. However, in riffles studied in detail, the average velocity was 0.39 m s⁻¹ (Gardeström et al., 2013). Stream slope was 1.5% (Palm, Unpublished data, 2012). Stream bed sediments are also variable in size, with small particles in pools and boulders in riffles. Cultivated boreal forest, predominated by Scots pine *Pinus sylvestris* L., Norwegian Spruce *Picea abies* L. and birch *Betula* spp. L., is surrounding the stream.

Production of genetic unique brown trout embryos

In October 2014, approximately 100 anadromous brown trout were caught at Norrfors fish ladder located close to the outlet of Ume river in the Bothnian bay (Fig. 1). Both females and males were caught and fish size ranged between 3-7 kg. Tissue samples from all individuals were collected whereafter the fish were placed in a holding tank. The tissue samples were analyzed for Single Nucleotide Polymorphism markers (SNPs) that would be transferred to potential offspring.

A SNP marker is a single base change at a specific place in a DNA sequence that usually occur with two different nucleotide combinations (Vignal et al., 2002). The least frequent combinations should occur in 1% of the genomes or more. By locating a number of SNP markers at a genome and compare the SNP markers among individuals it is possible to analyse relationships.

From the sample of 100 individuals, eight males and eight females were detected to have appropriate SNPs. Two weeks after being caught, these males and females were stripped of eggs and melt to produce eight sets of genetic unique offspring i.e. eight families. The

fertilized eggs were then kept under normal rearing conditions until the eyed stage. Egg stocking was then conducted.

Egg stocking

In March 2015, 33 084 eyed trout eggs were planted in the stream at three different stocking points, 86, 893, and 1 198 meters from Lake Österavan (Fig. 2). In total, eggs from eight different parent couples were planted (Table 1). Based on expected low catches, all eggs from each family were stocked in the same stocking point. In each stocking point a perforated basket (0.5*0.5*0.7 m) was placed on top of the stream bed. Four Whitlock-Vibert boxes were filled with spawning gravel and eyed eggs whereafter they were placed on the bottom of each basket. The boxes were covered with spawning gravel.

Table 1. Number off eggs from each family planted in each stocking point. The distance from the stocking points in relation to Lake Österavan is given in parenthesis.

Stocking point (location)					
1 (86 m)		2 (893 m)		3 (1 198 m)	
Family	No. of eggs	Family	No. of eggs	Family	No. of eggs
1	4 374	4	1 204	7	3 459
2	3 569	5	4 226	8	7 259
3	4 246	6	4 747		
Total	12 189		10 177		10 718

Sampling of YOY

The electrofishing was conducted on two occasions. During the first occasion, 24th-25th of August 2015, the whole study reach was electrofished using a battery driven back pack electroshocker (Hans Grass IG600, Hans Grass Inc., Germany) that produces a pulsing current of 600 V. All fish collected were identified to species. When a brown trout was caught it was kept in a hand net while a small section of the anal-fin was removed. The anal-fin samples were stored in alcohol. Brown trout body length was measured (mm) before the trout was returned to the stream. To keep the procedure quick no anesthesia was used. The distance (m), in relation to a fixed point along the stream, where each trout was caught was recorded.

Habitat data was collected on every 10th meter of the study reach. Mean stream bed particle size and depth in the center of the stream was estimated and the velocity was categorized in four classes: pool, run, riffle without white water, and riffle with white water.

The second electrofishing occasion took place on the 21st-22nd of September 2015 using a more effective generator-powered electroshocker (Lugab, Luleå, Sweden) that produced a constant direct current of 800 V. The fish sampling procedure in September was performed the same as the fish sampling procedure in August with the exception that only the upper part of the reach – from Lake Österavan and 389 m downstream was sampled. The fish sampling in August occurred about eight weeks after the end of swim-up and the fish

sampling in September about 12 weeks after the end of swim-up. Swim-up should last for around 20 days and occur in June (Palm, Unpublished data, 2003).

DNA analysis

A DNA analysis was performed on selected fin samples to determine which egg planting site and which parents the individual originated from. SNPs were used in the analysis.

DNA was extracted from alcohol preserved fin samples using QIAasympphony[®] DSP (QIAGEN[®]) following the manufacturer's instructions. A 87 SNP panel constructed for trout by Wirén et al. (submitted) at VFM, SLU was used for genotyping. Genotyping was performed with a Biomark[™] HD (FLUIDIGM[®]) according to the user's guide. The software ML-RELATE (Kalinowski et al., 2006) was used to estimate relatedness between parent and offspring individuals, and to conclude which parent each offspring originates from.

Data analysis

Three outliers, one individual from family 6 and two individuals from family 8, which had dispersed very long distances, were excluded from the analysis. To test if families differ in body length separate Analysis of Variance (ANOVA)-models were used for each stocking point.

ANOVA was also used to determine if family and direction of dispersal had an effect on the distance dispersed. Separate models were used for each stocking point and if a significant effect was found Tukey multiple comparison of means was used. To test the effect of body length on dispersal distance, a general Linear mixed effects model was used on data from the fish sampling in August, treating dispersal distance as a response variable and length as a fixed effect. To account for dependence between observations within each stocking area the stocking point was treated as a random factor. For the same test a Linear model could be used on the data from September since only trout from one stocking point were included in the analysis.

Prior to the habitat analyses (number of YOY vs. sediment, depth, and velocity) the stream was divided in 10 m (linear stream length) cells and the number of trout in each cell was summarized. Linear models were used when analyzing the effect of sediment and depth on the number of YOY in each stream cell. To test the effect of velocity on number of YOY, ANOVA was used treating velocity as a four level factor. If a significant effect was found, Tukey multiple comparison of means was used to further explore the effect.

The data analysis was performed with the analytical software R (R Core Team, 2014) including the package nlme (Pinheiro et al., 2014).

Results

During electrofishing a total of 433 brown trout was caught. Although the electrofishing was focused on brown trout, approximately 30% more bullhead was caught. Also scattered individuals of perch, burbot, pike, common roach, and brook lamprey was caught. The general expression was that brown trout was associated with stream marginal habitat.

Family and YOY body length

Body length of the individuals did not differ significantly between families in either of the

three stocking points during fish sampling in August (Table 2). Stocking point 1 (Anova: $F_{2,31}=1.496$, $p=0.240$), stocking point 2 (Anova: $F_{2,32}=0.716$, $p=0.497$), stocking point 3 (Anova: $F_{1,21}=2.113$, $p=0.161$). The same was found for body length in September (Anova: $F_{2,87}=2.556$, $p=0.083$) (Table 3).

Table 2. Average body lengths of YOY brown trout in August.

Stocking point	1			2			3	
Family	1	2	3	4	5	6	7	8
Average body length (mm)	93	98	89	89	86	86	91	85

Table 3. Average body lengths of YOY brown trout in September.

Stocking point	1		
Family	1	2	3
Average body length (mm)	106	106	100

Family and dispersal distance

During fish sampling in August the effect of family on dispersal distance was only detected in stocking point 2 (Anova: $F_{2,32}=4.380$, $p=0.021$) between family 4 and 6 (Tukey multiple comparisons of means: $p=0.056$) and family 5 and 6 (Tukey multiple comparisons of means: $p=0.042$) (Fig. 3). Family did not have a significant impact on the distance dispersed by YOY from stocking point 1 (Anova: $F_{2,31}=1.343$, $p=0.276$) or 3 (Anova: $F_{1,21}=0.074$, $p=0.788$).

Analysis of data from the fish sampling in September, which only included individuals from stocking point 1, did not reveal any significant effect of family on the distance dispersed (Anova: $F_{1,88}=0.033$, $p=0.856$) (Fig. 4). Mean distances dispersed by each family are presented in Table 4-5.

Three individuals that were treated as outliers in the analysis had dispersed extremely long distances upstream, one individual from family 6 had dispersed 550 m and two individuals from family 8 had dispersed 940 m and 1 199 m respectively.

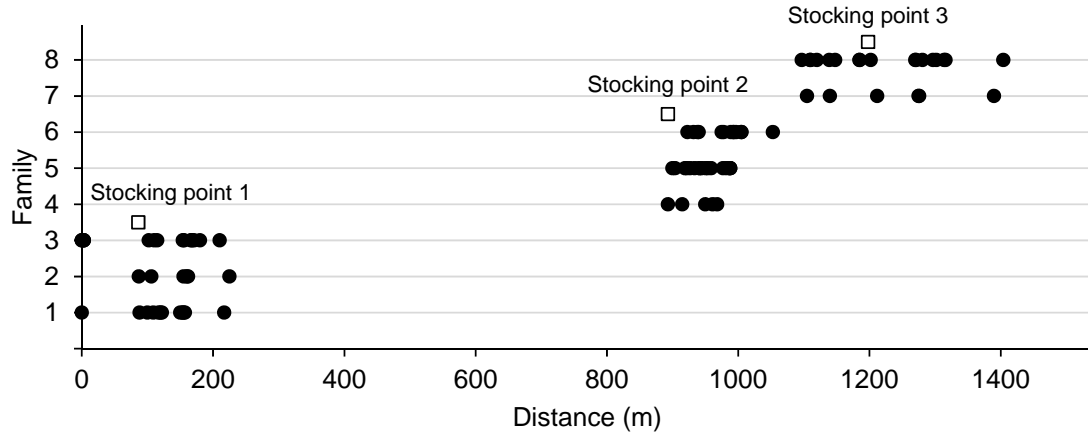


Figure 3. Data from fish sampling in August. Each black data point indicates the family and location of the DNA-sampled YOY brown trout individual. Individuals that were located in the same distance from Lake Österavan and belonged to the same family are represented as one single data point. The squares indicate the stocking points. Distance is from Lake Österavan.

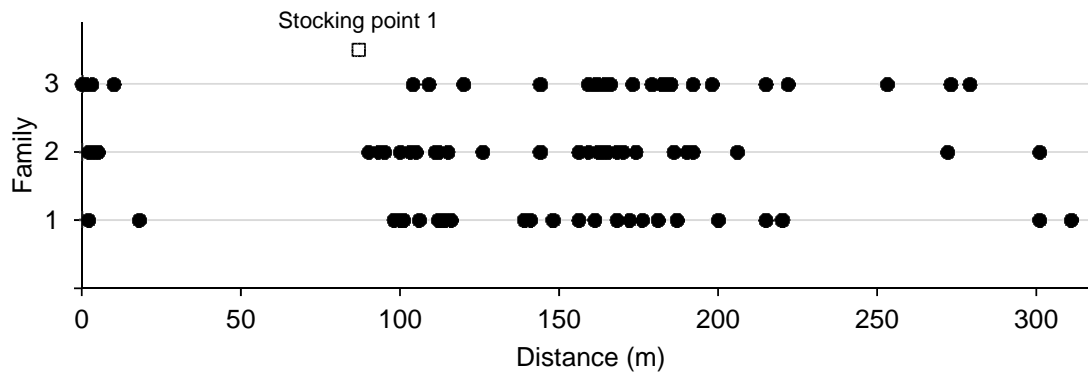


Figure 4. Data from fish sampling in September. Each black data point indicates the family and location of the DNA-sampled YOY brown trout individual. Individuals that were located in the same distance from Lake Österavan and belonged to the same family are represented as one single data point. The square indicates stocking point 1. Distance is from Lake Österavan.

Table 4. Data from fish sampling in August. Number of YOY brown trout, mean and maximum distances dispersed, and percentages of individuals dispersed up- or downstream in each stocking point and family. One individual from family 4 was located at the stocking point, therefore has only 80% of the trout dispersed.

Stocking point	1			2			3	
Family	1	2	3	4	5	6	7	8
Number of trout	12	7	15	5	17	13	6	17
Mean dispersal distance (m)	52	64	73	44	55	86	85	80
Dispersed upstream (%)	8	0	33	0	0	0	33	47
Dispersed downstream (%)	92	100	67	80	100	100	67	53
Max upstream distance (m)	86	-	86	-	-	-	93	101
Max downstream distance (m)	131	139	124	75	95	160	192	206

Table 5. Data from fish sampling in September. Number of YOY brown trout, mean and maximum distances dispersed, and percentages of individuals dispersed up- or downstream in each stocking point and family.

Stocking point	1		
Family	1	2	3
Number of trout	25	32	33
Mean dispersal distance (m)	76	71	94
Dispersed upstream (%)	8	13	21
Dispersed downstream (%)	92	88	79
Max. upstream distance (m)	85	85	87
Max. downstream distance (m)	224	87	192

Mean downstream travelled distance in August (all individuals pooled) was 68 m and mean upstream travelled distance was 72 m. In September, mean downstream travelled distance was 80 m and mean upstream travelled distance was 83 m. When pooling all individuals in both August and September, 97% of the downstream dispersers stayed in a distance of 200 m from the stocking point and 97% of the upstream dispersers stayed within a distance of 100 m.

Direction of dispersal and dispersal distance

The direction of dispersal did not show any significant effect on the distance dispersed in either of the stocking points in August, stocking point 1 (Anova: $F_{1,32}=2.643$, $p=0.114$)

stocking point 3 (Anova: $F_{1,21}=2.352$, $p=0.140$) (individuals from stocking point 2 had only dispersed downstream). The dispersal direction in September didn't either show a significant effect on the distance dispersed (Anova: $F_{1,88}=0.037$, $p=0.848$).

Body length and dispersal distance

The body length of the individuals did not have a significant effect on the dispersal distance in either August (linear mixed-effects model: $F_{1,88}=2.306$, $p=0.133$) (Fig. 5) or September (linear model: $F_{1,88}=0.945$, $p=0.334$) (Fig. 6).

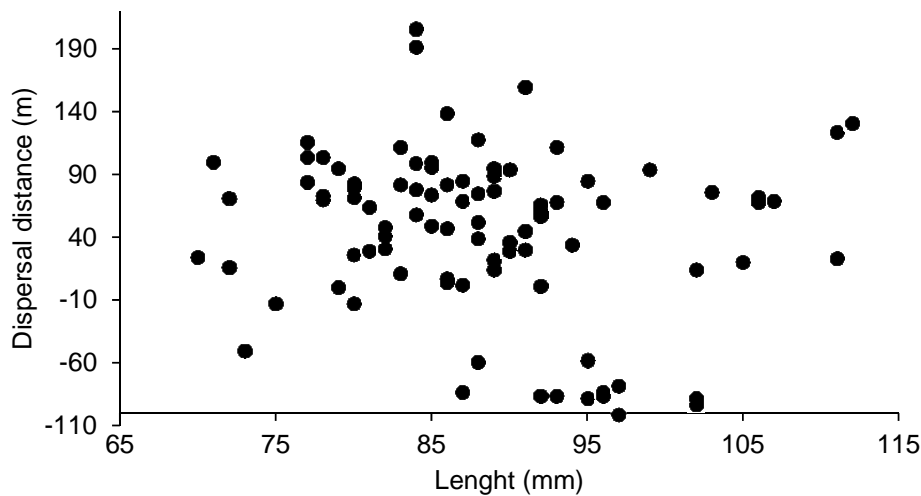


Figure 5. YOY brown trout dispersal distances from stocking points in August plotted against body length. Positive numbers indicate downstream dispersal and negative numbers upstream dispersal.

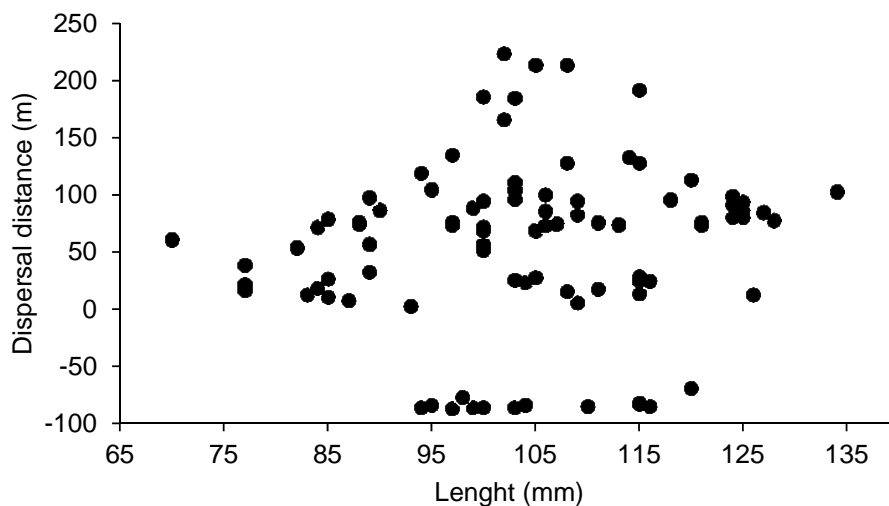


Figure 6. YOY brown trout dispersal distances from stocking points in September plotted against length. Positive numbers indicate downstream dispersal and negative numbers upstream dispersal.

Habitat characteristics and abundance of trout

Stream bed particle size

Stream bed particle size was found to have a significant effect on the number of YOY in each 10 m cell in both August (linear model: $F_{1,152}=22.220$, $p<0.001$) and September (linear model: $F_{1,37}=17.960$, $p<0.001$). More YOY trout could be found in habitats with coarser substrate sizes (Fig. 7-8).

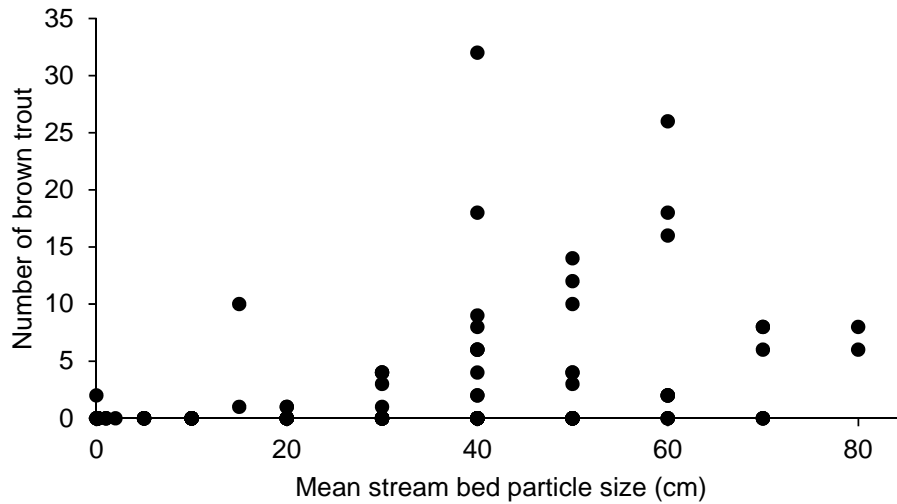


Figure 7. Relationship between numbers of caught YOY brown trout in each 10 m stream cell and mean stream bed particle size in the center of each cell. Data is from fish sampling in August.

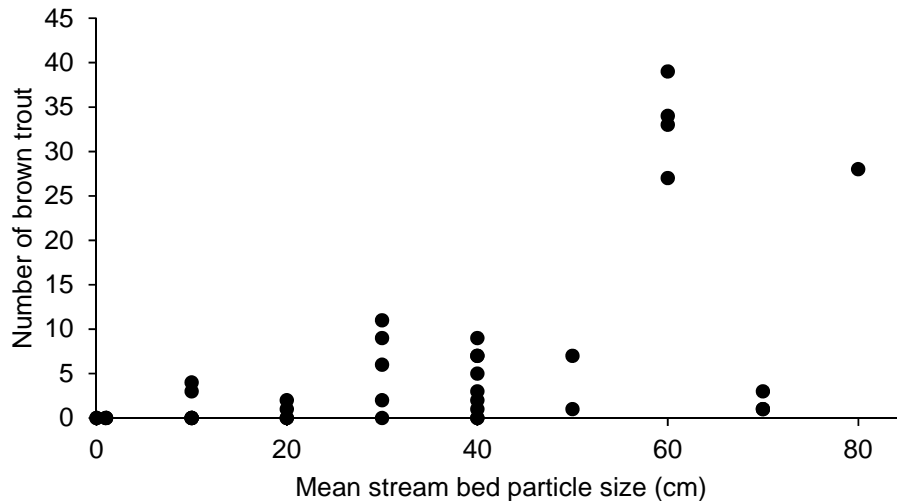


Figure 8. Relationship between numbers of caught YOY brown trout in each 10 m stream cell and mean stream bed particle size in the center of each cell. Data is from fish sampling in September.

Depth

Depth had a significant effect on the number of YOY in each 10 m stream cell in August and September (linear model: $F_{1,152} = 8.279$, $p < 0.01$; linear model: $F_{1,37} = 5.353$, $p = 0.026$). Less YOY trout could be found at deeper water (Fig. 9-10).

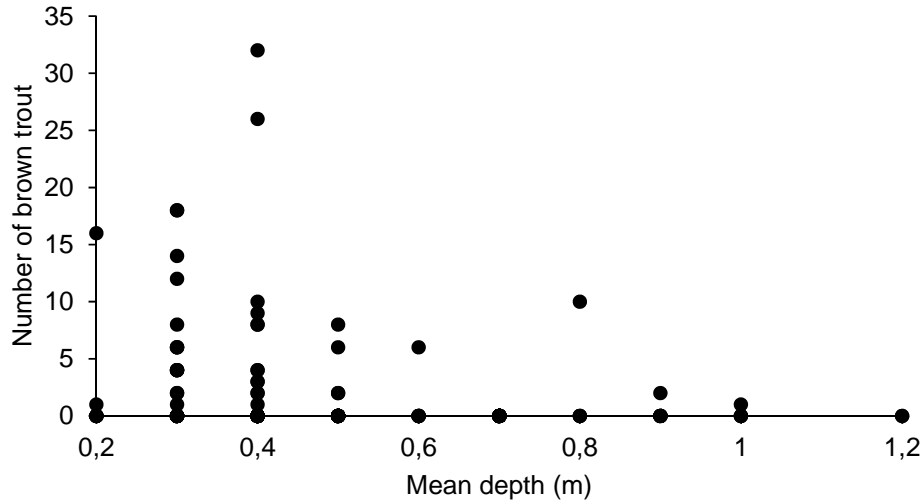


Figure 9. Relationship between numbers of caught YOY brown trout in each 10 m stream cell and mean depth in the channel center of each cell. Data is from fish sampling in August.

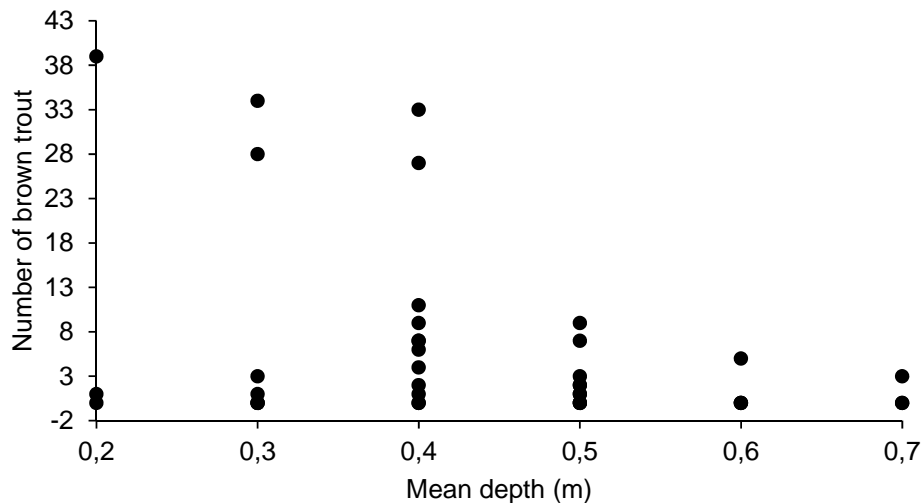


Figure 10. Relationship between numbers of caught YOY brown trout in each 10 m stream cell and mean depth in the channel center of each cell. Data is from fish sampling in September.

Velocity

Velocity had a significant effect on the number of YOY in each 10 m stream cell in August (Anova: $F_{3,150} = 3.970$, $p < 0.01$). The number of YOY trout in pool habitat was lower than the number of YOY trout in riffle without white water habitat (Tukey multiple comparison of

means: $p=0.041$) (Table 6, Fig. 11). In September on the other hand, velocity did not have a significant effect on the number of YOY trout (Anova: $F_{3,36}=2.213$, $p=0.103$) (Table 7, Fig. 12).

Table 6. Total number of caught YOY brown trout in sections with different velocity. 1= pool, 2= run, 3= riffle without white water, 4= riffle with white water. Data is from fish sampling in August.

Velocity class	1	2	3	4
Number of trout	0	83	171	21

Table 7. Total number of caught YOY brown trout in sections with different velocity. 1= pool, 2= run, 3= riffle without white water, 4= riffle with white water. Data is from fish sampling in September.

Velocity class	1	2	3	4
Number of trout	0	45	179	38

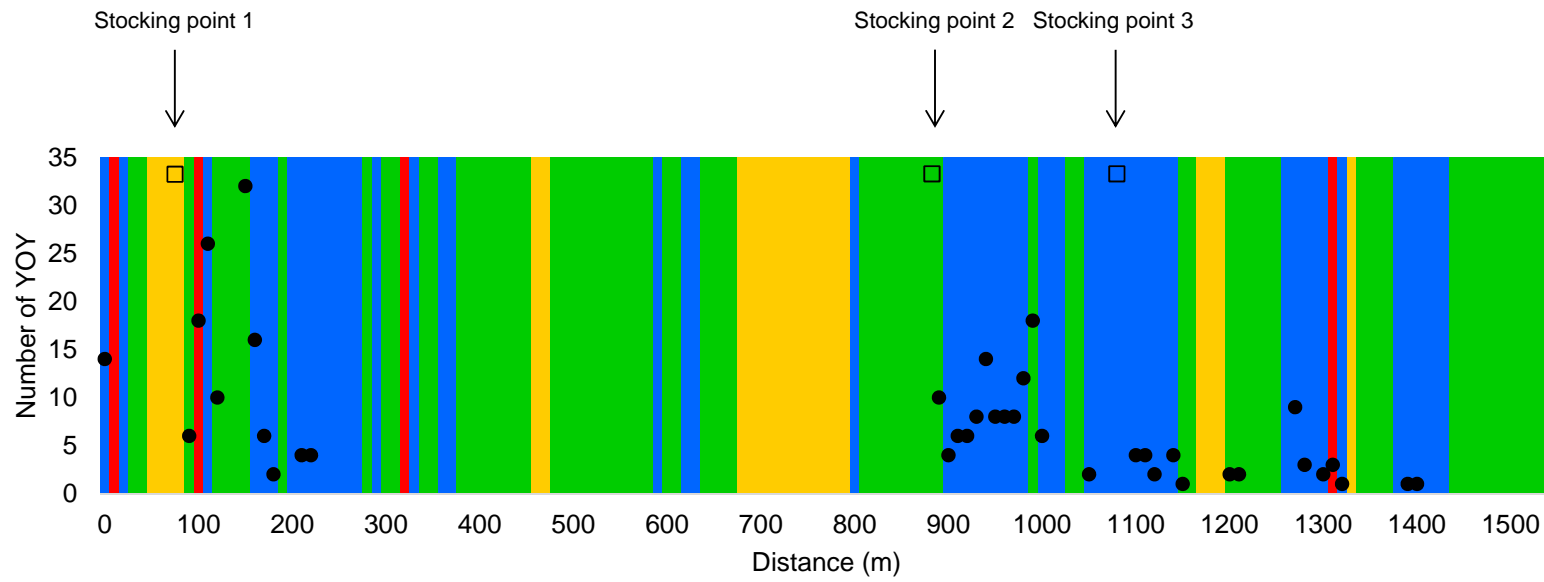


Figure 11. Number of caught YOY brown trout in each 10 m stream cell. Color of the field indicates velocity classification. Yellow = pool, Green = run, Blue = riffle without white water, Red = riffle with white water. Distance is measured from Lake Österavan. Data is from fish sampling in August.

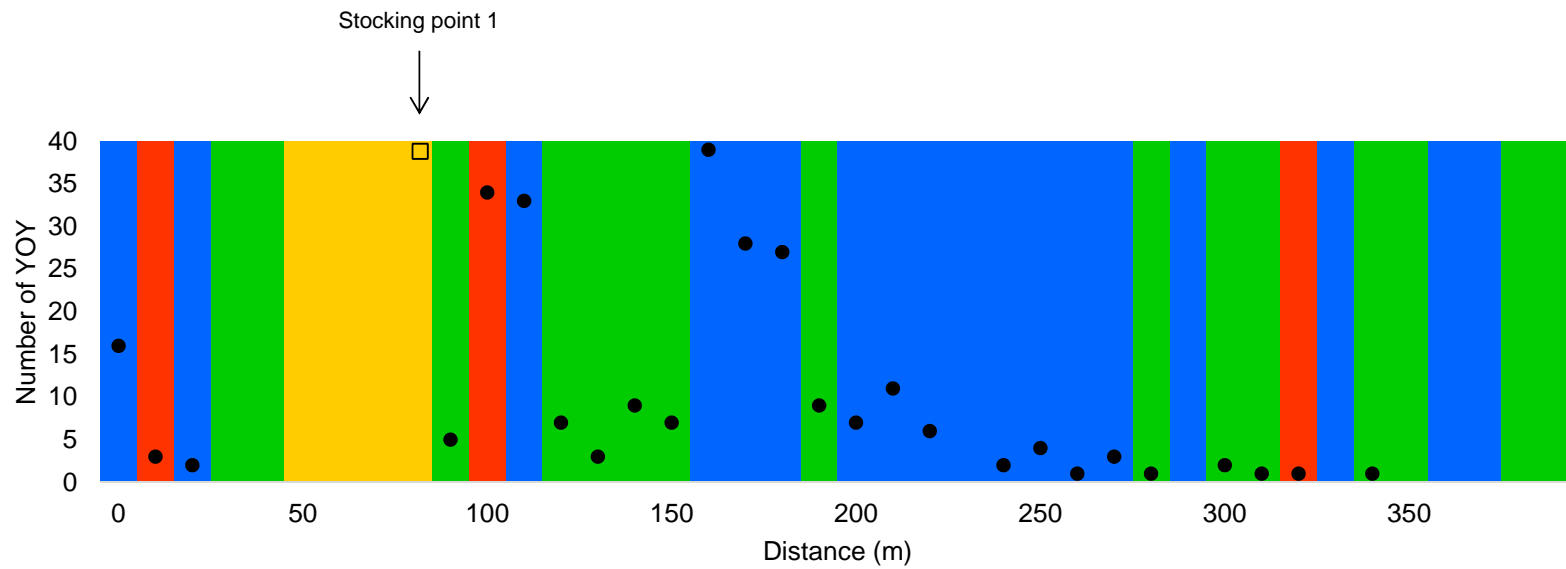


Figure 12. Number of caught YOY brown trout in each 10 m stream cell. Color of the field indicates velocity classification. Yellow = pool, Green = run, Blue = riffle without white water, Red = riffle with white water. Distance is measured from Lake Österavan. Data is from fish sampling in September.

Discussion

Dispersal of YOY trout in the study stream clearly followed distinct patterns. The results showed that body length did not have an impact on dispersal distance and that family only had an impact in one of the three stocking points. Water velocity, stream bed particle size, and stream depth also impacted YOY dispersal from the stocking point. The results of this study are discussed below in relation to previous findings and in relation to practical management by addressing the following four questions.

Did YOY trout disperse differently between families?

Only one family (family 6, stocking point 2) showed a different dispersal pattern than the other families originating from the same stocking point. Family 6 had dispersed further downstream than the other families. Also, none of the individuals from family 6 stayed in the direct vicinity of the stocking point, as individuals from all other families did at the first fish sampling in August. These results are interesting as they differ from what Héland (1980), Heggenes and Traaen (1988) and Webb et al. (2001) found.

Webb et al. (2001) found a general interaction between family and dispersal distance in Atlantic salmon fry 17 weeks after hatching. The relative abundance of individuals in relation to distance downstream from the stocking point varied between the families. García de Leaniz et al. (2000) found that developmental stage and date of swim-up varied in full-sibs of newly emerged Atlantic salmon fry. Potentially this early variation generates a big variation in body length of YOY full-sibs. Webb et al. (2001) discovered that YOY body length was largest close to the stocking point and that the length decreased with distance downstream to about 100-150 meters. Héland (1980) also found that trout fry that dispersed downstream were smaller than non-migrants. Also Heggenes and Traaen (1988) pointed out that the tendency for fry to be swept away downstream was higher for smaller individuals.

The data from this study revealed no relationship between YOY body length and family origin or YOY body length and dispersal distance. Individuals of varying size had dispersed both long and short distances from the stocking point. Body length could therefore not explain differing dispersal distance of family 6.

Maybe the differing result in the present study depends on the body length of the investigated trout. Potentially the body length of YOY in this study was long enough to withstand displacement by high water velocity. For instance the mean body length of the two groups of trout included in the study by Heggenes and Traaen (1988) were c. 32 mm and c. 43 mm and the salmon in Webb et al. (2001) were c. 48 mm. This compared to trout in the present study that had a body length of 85-98 mm in August and 100-106 mm in September.

Was YOY trout dispersal restricted to a limited area?

It was clear that YOY trout mainly disperse downstream. This correspond with the result in several other studies (e.g. Beall et al., 1994, García de Leaniz et al., 2000, Daufresne et al., 2005). Regarding dispersal distance the result showed that almost all (97%) of the downstream dispersers stayed within a distance of 200 m downstream from the stocking point and that the majority (97%) of the few individuals that dispersed upstream stayed within a distance of about 100 m. As no earlier studies have investigated dispersal distances of brown trout in the same age span as in the present study, comparable data is lacking. However, similar studies have been conducted on Atlantic salmon (Beall et al., 1994, Webb et al., 2001). These studies reported a slightly longer dispersal distance compared to this

study. Beall et al. (1994) studied salmon that hatched in March and observed 71% of them located downstream from the stocking point within a distance of 200 m in the beginning of April, while 68% was observed downstream within a distance of 900 m in mid-June. Webb et al. (2001) detected most of the individuals within 380 m downstream from the stocking point. The salmon in their study were a few weeks older than the trout in this study. It might be that Atlantic salmon naturally disperse longer distances from the redd compared to trout but it might also be explained by water velocity since slopes of the study streams were higher in the latter studies (Stream slope was 11% in Beall et al. (1994). In Webb et al. (2001) the stream was fast flowing with a slope of 6% while in the present study stream slope was only 1.5%). Thus it is presumable, since water velocity has a positive relationship with downstream dispersal, that the steeper slope had a positive effect on the distance dispersed. In the study stream, riffles contained large amounts of big boulders which might have further shortened the dispersal distance by creating refuges from strong velocities.

While the maximum dispersed distance upstream was 90 m in the study by Webb et al. (2001) the maximum dispersed distance upstream in this study was 1 199 m. On the other hand their maximum downstream dispersed distance was 940 m while maximum downstream distance was only 224 m in this study. It is hard to find any reasonable explanation to why only three individuals dispersed exceptionally long distances upstream. It might partly be explained by attempts to search for more nutritious water closer to the outlet of Lake Österavan since Klemetsen et al. (2003) states that this kind of movement might start just after emergence. Knowing that no resident trout were present in the stream at the start of this study we can conclude that the YOY trout restricted dispersal distances are not a consequence of competition by resident trout.

Did mesoscale flow and habitat characteristics influence YOY trout dispersal?

From the result it is clear that the YOY trout avoid pool habitat and prefer riffles. Riffles without white water was the habitat with highest numbers of caught YOY. Stream bed particle size showed a positive relationship with the number of trout while stream depth showed a negative relationship with the number of trout.

The study of juvenile trout habitat preference conducted in a stream in the north-eastern parts of Finland revealed similar results as this study concerning YOY depth preference (Mäki-Petäys et al., 1997). Habitat containing more trout in size-class 4-9 cm in autumn had a depth of 0.15-0.35 m and most trout in this study were observed in habitats with a depth of 0.3-0.4 m. In Mäki-Petäys et al. (1997), depth was measured at the same location as the trout was observed, while depth in this study was estimated in the middle of the stream channel, thus depth might be a bit overestimated in this study. Mäki-Petäys et al. (1997) also found that during summer and autumn trout in the two smallest size-classes (4-9 cm and 10-15 cm) were found in habitats with particle sizes in roughly the same proportion as they were presented in the stream, but seemed to have a slight preference for habitat with finer stream bed particles size. This does not agree with results of this study since more trout could be found at coarser stream bed particle sizes.

Elliott (1987) states that the stream bed structure is an important factor concerning the distance dispersed as it can provide the trout with low-velocity refuges. However, water velocity is an even more important physical factor considering downstream movement of YOY (Elliott, 1987). In accordance with other studies (Heggenes et al., 1999 and references therein), this study shows that young trout prefer riffles with moderate water velocities. Since a four level classification of the velocity was used in this study there are no absolute velocity values to compare with the earlier studies.

From observations in the field it seemed like more trout were located close to the stream banks where the velocity was lower than in the mid-channel. The explanation to this could be an optimal velocity for drifting prey and the ability to withstand the current as well as the high abundance of bullhead. Roussel and Bardonnnet (1999) detected a similar pattern, especially during night but also during daytime, in habitats that had a high abundance of bullhead.

Upstream from stocking point 2 there is a long (250 m) section of run and pool habitat. It seems like this reach of the stream acts as a dispersal barrier since only three individuals (the outliers) have managed to pass it and no individuals were observed in this reach even if stocking point 2 was located next to it. Stream bed particle size was low in the slow flowing parts of the stream. Thus, it might be hard for trout to find low velocity refuges and shelter to hide from predators such as pike and perch, which were observed in the pools. Likewise to YOY in our study which used reaches with many boulders, the smallest and youngest trout in a study by Jonsson (1989) used the most sheltered habitats to avoid predation. Larger particle sizes also create the earlier mentioned low-velocity refuges where the trout can save energy while feeding (Bardonnnet and Heland, 1994, in Heggenes et al., 1999). The general pattern observed in this study is that the majority of YOY trout disperse from the redd to a neighboring riffle while a small fraction disperse to run habitat.

However, it is important to mention that the trout in this study only were observed during day-time in August and September. Habitat use can vary depending on season (Mäki-Petäys et al., 1997) and time of the day (Roussel and Bardonnnet, 1999).

This study was conducted in a stream where no trout were present at the start of the study. The abundance of available niches and resources was probably high. If the study would have been conducted in a stream with an already present trout population and less resources the dispersal pattern could have been different. In August, few individuals of family 2, 4, and 7 was caught. More individuals would have been beneficial to improve the quality of the data. Also, in September we only sampled the upper part of the study reach, adjacent to stocking point 1. It would have been interesting to investigate if the dispersal differed between families from stocking point 2 and 3 in September.

Do trout managers need to consider YOY trout dispersal patterns for successful restoration?

There are few studies evaluating the results of egg stocking. However, in a study of egg stocking success Syrjänen et al. (2015) found that egg stocking in order to enhance populations of brown trout in the Finnish rivers was rather ineffective. They state that one contributing factor to unsuccessful egg stocking could be placing of egg boxes in unsuitable microhabitat causing unnatural high mortality. One explanation could be that these microhabitats don't have the necessary water current needed to supply the embryos with oxygen.

Given the observed patterns of YOY trout dispersal in the present study, some aspects need to be considered for successful trout management in restoration projects. It is clear that YOY brown trout have restricted dispersal. They avoid pool habitat and prefer riffles. This should be taken into account when selecting stocking points in habitat restored streams.

First, as dispersal is restricted to certain distances, stocking points should be located with consideration to these distances to maximize the use of habitat. Results in this study suggest

that a distance of 300 m should be sufficient to prevent individuals from different stocking points competing for the same habitat.

Second, as flow and habitat characteristics clearly influence dispersal, stocking points should also be located with consideration to this. Since pool habitats seem to restrict the dispersal of YOY trout, egg stocking points should not be allocated in direct vicinity of these habitats. Also, YOY trout prefer riffle-habitats, especially those without white water, i.e. not fast flowing riffles, thus it is preferable if the stocking points are located in vicinity of these habitats. Fry are poor swimmers after swim-up (Elliott, 1987) and the lowest critical velocity for emerging trout is around 0.15 m s^{-1} in 6-8 °C and 0.19 m s^{-1} in 12-14 °C (Heggenes and Traaen, 1988). The egg stocking point should not be placed in velocities exceeding the lowest critical velocity to avoid downstream displacement of emerging fry. The best option would be to place the eggs in a stream habitat with connection to a slow-flowing riffle without pools nearby.

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